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A unified framework for plant life history strategies shaped by fire and herbivory

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Summary:

Fire and herbivory both remove above-ground biomass. Environmental factors determine the type and intensity of these consumers globally, but the traits of plants can also alter their propensity to burn and the degree to which they are eaten. To understand plant life history strategies associated with fire and herbivory we need to describe both response and effect functional traits, and how they sort within communities, along resource gradients, and across evolutionary timescales. Fire and herbivore functional traits are generally considered separately but there are advances made in understanding fire which relate to herbivory, and vice versa. Moreover, fire and herbivory interact: the presence of one consumer affects the type and intensity of the other. Here we present a unifying conceptual framework to understand plant strategies that enable tolerance and persistence to fire and herbivory. Using grasses as an example, we discuss how flammability and fire tolerance, palatability and grazing tolerance traits, might organise themselves in ecosystems exposed to these consumers, and how these traits might have evolved with reference to other strong selective processes like aridity. Our framework can be used to predict both the diversity of life history strategies and plant species diversity under different consumer regimes.

Keywords: flammability, grass, herbivory, palatability, plant defence, plant functional traits, tolerance, trophic ecology

Introduction:

Globally, fire and large mammal herbivores are two major consumers of above-ground plant biomass, particularly in tropical ecosystems where they are important drivers of plant evolution and vegetation structure (Bond, 2005). Empirical evidence demonstrates that fire-adapted and herbivore-adapted plant communities in the same abiotic environments differ in species composition, structure and plant functional traits (Collins & Barber, 1986; Anderson *et al.*, 2007; Forrestel *et al.*, 2015; Kruger *et al.*, 2017). Indeed, fire and herbivory can be seen as ecological filters where organisms exposed to these consumers must possess attributes enabling persistence and reproduction, or they will be lost from a community (Belsky, 1992; Cingolani *et al.*, 2005). A substantial literature both in trophic and fire ecology exists, but these bodies of research have developed independently with different theoretical approaches. Fire is seen as a disturbance, whereas herbivory can be considered in terms of predator-prey dynamics, but neither of these theoretical frameworks is entirely satisfactory – see McNaughton (1983) for a discussion on this for herbivory, and Evans (1989) for fire. There are several reasons why it would be beneficial to contrast these two ecological drivers as 'consumers' of vegetation (Bond & Keeley, 2005) in a common framework. Firstly, individual plants are often exposed to both fire and herbivory over their lifetime. Secondly, the intensity and frequency of fire and herbivory depend to some extent on vegetation properties (Burkepile *et al.*, 2013; Platt *et al.*, 2016). Therefore, unlike a disturbance such as drought, there can be feedbacks between community composition and these consumers that can act either to promote or reduce their intensity. Finally, unlike most predator-prey relationships, it is possible for individual plants to survive, or even benefit from a consumption event (Strauss & Agrawal, 1999; Gagnon *et al.*, 2010).

Through the removal of above-ground biomass both fire and herbivory can alter competitive interactions within communities by enabling tolerant plants to remain in environments where less-tolerant plants – but better competitors – would otherwise dominate (Collins & Barber, 1986; Cingolani *et al.*, 2005). Intense consumption can alter the architecture of plants, where less intense consumption simply removes leaf material (Danell *et al.*, 1994). Fire is episodic and it is rare for an ecosystem to sustain more than one fire per year (usually every 2-5 years in tropical grasslands and savannas, and much less frequently elsewhere (Archibald *et al.*, 2013a)). Some insect herbivory is also episodic, but many other herbivores are always present, and it is possible to be exposed to repeated, frequent defoliation from herbivores within a day, week and year (McNaughton, 1983). With fire, plants need to protect remaining, unconsumed living material from extreme heat, whereas with herbivory plants need

to be able to withstand the physical action of tugging and breaking of the plant. Moreover, as fire is a physical process requiring energy, heat, and oxygen, and herbivory is a biological process requiring energy, water and a range of other essential nutrients, these two consumers, while both consuming above-ground biomass, are not necessarily attracted to the same plant parts or plant traits.

Here, we contrast the approaches of fire and trophic ecology integrating these parallel fields of research to define a unified theoretical framework that enables predictions about community assembly and the viability of plant ecological strategies with varying regimes of fire and herbivory. Using grasses as an example, we identify plant functional traits associated with resistance and tolerance of fire and grazing, versus attraction and avoidance of fire and grazing. We use our proposed framework to assess the extent to which adaptations to fire and mammalian herbivory are compatible (i.e., result in the same plant functional types), or antagonistic (select for different plant life histories) and how this might have affected community assembly and therefore plant evolution. We discuss what this means for the structure and dynamics of ecological communities exposed to these consumers, and how these adaptations interact with other environmental drivers such as aridity and cold temperatures. Finally, we consider whether and how the plant traits and life histories identified here relate to other theoretical frameworks in the broader plant trait and plant economics literature.

Why grasses? Poaceae is a diverse family of over 11000 species that dominate the ground layer of ~40% of the Earth's land surface, covering environments ranging from extreme heat and aridity to below freezing (Linder *et al.*, 2017). In expanding to cover their current geographical range grass species evolved functional characteristics that enabled survival under many combinations of fire, herbivory, drought, light availability, water logging and low temperatures. Grasslands burn frequently and support large numbers of livestock and/or indigenous animals (Lehmann & Parr, 2016). There are several examples where removing herbivores from an ecosystem increases fire frequency, indicating competitive interactions between fire and herbivory that are mediated by the composition and functional traits of the grass community (Johnson et al 2018). Poaceae is therefore a useful model for integrating understanding of how adaptations to fire and herbivory have emerged from and interact with other dimensions of the environment.

Contrasting current theoretical approaches in trophic vs fire ecology

In the trophic ecology literature tolerance is generally defined as "the degree to which plant fitness is affected by herbivore damage relative to fitness in the undamaged state" (Strauss & Agrawal, 1999). Resistance is a separate concept: "any plant trait that reduces the preference or performance of herbivores". Other authors use different terms for the same concepts (Table 1), but it is generally agreed that these represent alternative life history strategies – i.e. plants with traits that make them unlikely to be eaten are not expected to have traits that confer tolerance (van der Meijden et al., 1988, although see Núñez-Farfán et al. (2007) for further discussion).

Theory has been developed to predict when it would be beneficial for plants to invest resources in avoiding herbivory (Feeny, 1976; Coley *et al.*, 1985; Herms & Mattson, 1992). The converse, that plants might require herbivory in order to be fit, and that attracting herbivores could be advantageous, has also been debated (McNaughton, 1983, 1986; Janzen, 1984; Belsky, 1986) but the focus has been on consequences for productivity (overcompensation) rather than overall fitness (Belsky *et al.*, 1993). De Mazancourt (2001) demonstrated that plant-herbivore mutualisms were possible, but only in very restricted circumstances, and this has not been formulated in terms of individual-level selection for palatability per se.

In the fire ecology literature, in contrast, there has been more focus on the mechanism by which species persist in a fire-prone environment. Plants can resist fire (i.e. not be damaged by a fire event), they can avoid fire (i.e. not be burned in a fire event), or they can be burned in a fire event, and regenerate either from resprouting (individual level persistence) or from seed (population level persistence) (Whelan, 1995; Gignoux *et al.*, 1997; Pausas & Lavorel, 2003). In the fire literature there has also been discussion on the degree to which flammability, or the lack thereof, interacts with fire tolerance strategies: flammable plants have associated tolerance traits, and less flammable plants tend to show resistance (Schwilk & Ackerly, 2001). Moreover, flammability has been proposed to increase individual fitness through directing heat away from sensitive plant parts (Gagnon et al., 2010 - individual-level) or creating a better environment for offspring by damaging other plants (Bond and Midgley, 1995 - population level), and could therefore be selected for, although there are those that argue that flammability is simply an emergent property of selection for other plant functions related to leaf economics (Midgley, 2013). See Pausas (2017) for an extensive review of this topic.

Some herbivore ecologists are more aligned in their terminology to fire ecologists. Briske (1996), for example, defined "avoidance" as the ability to reduce the probability of being eaten (resistance in Strauss and Agrawal's (1999) formulation), and then defined resistance as a concept which integrates both strategies to determine whether a plant can persist and reproduce in the face of a disturbance. Moreover, defence has sometimes been used as an umbrella-term incorporating both tolerance and resistance, and elsewhere used synonymously with resistance (Stowe *et al.*, 2000; Fornoni, 2011).

An integrated framework

We suggest that some of these confusions can be resolved by distinguishing between the ability to avoid a defoliation event all together – i.e. be unpalatable or non-flammable, and the ability to "resist" a defoliation event when it happens by protecting sensitive plant parts (Box 1). These two concepts are usually conflated into 'plant defence strategies' (e.g. Agrawal, 2011), but are quite different ecologically. The ability to "resist" defoliation is a subset of a range of plant tolerance strategies to defoliation, and says nothing about an individual plant's attractiveness to herbivores or fire (i.e. the probability of being eaten/burned). For example Acacia species in African savannas with palatable leaves are also highly defended by spines to prevent too much biomass being removed (Charles-Dominique *et al.*, 2017), i.e. while they do not **avoid** herbivores, they **resist** them.

Once avoidance is clearly distinguished from resistance then it is easy to see plant life histories as existing on an axis from "avoidance" to "attraction" of fire or herbivory, and that where a plant sits on this axis affects the degree to which it is exposed to consumption, and therefore, the strategies that it requires to persist in a community exposed to fire or herbivory.

We therefore propose that when considering fire/herbivory adaptations there are three distinct axes, associated with three distinct functions which act over three distinct time periods that need to be quantified for understanding plant lift history strategies (Figure 1, Box 1). First is the "avoidance--attraction continuum" which acts before a plant is defoliated and determines whether a defoliation event is likely to occur. Second is the "resistance" continuum, which acts during the defoliation event, and determines the amount and type of biomass that is damaged or lost by the event. Finally, the "tolerance/persistence" continuum acts over the lifetime of the plant and beyond, integrating an individual plant's response to defoliation and whether a population and species can persist when exposed to a particular level/type of consumer.

As discussed by Strauss and Agrawal (1999), a plant's location on the avoidance-attraction continuum should strongly influence the type of plant resistance and tolerance traits that will be successful in a given environment, i.e. not all portions of these three axes will be occupied, but by placing plants on these axes it is possible to identify all possible strategies for surviving and persisting in consumer-prone environments. This different approach (Figure 1) integrates ideas from both fire ecology and trophic ecology, and should be able to be applied in both contexts. It both resolves confusion over avoidance vs resistance herbivore defences, and incorporates the idea that **even the most tolerant plant needs to resist at some level** – i.e. some part of its growth form needs to be protected from damage for recovery to occur.

Moreover, once both fire and herbivore adaptations are viewed from this combined framework, it should be possible to assess the degree to which adaptations for each consumer are aligned, or whether they select for different types of organisms – for example, is it possible to evolve traits that allow a plant to resist both fire and herbivory, or are there trade-offs such that fire-adapted species are more susceptible to herbivory and vice versa?

Contrasting avoidance-attraction traits for fire and herbivory in grasses

The differences between fire and herbivory become very clear when one considers which traits are associated with palatable vs flammable grasses. Fire burns more easily through dry grasses, with a high energy content (high C:N ratio), because these are easier to ignite and sustain a fire (Simpson *et al.*, 2016). Moreover, thin leaves arranged in an aerated canopy increase ignitability and fire spread rate (Schwilk, 2015). Low phosphorus content and the presence of volatile oils (Scarff & Westoby, 2008; Ormeno *et al.*, 2009) have also been shown to increase flammability.

In contrast, leaves with a high moisture content are preferred by grazers, as this minimises dependence on external water sources (Jarman, 1973), and is associated with actively growing leaf material with higher crude protein levels (Murray & Brown, 1993). Indeed, grazers prefer forage with a low C:N ratio, which is more digestible, and also high phosphorus content, as these nutritional components are required as part of a balanced diet that optimally supports metabolic processes (Owen-Smith & Novellie, 1982). Large leaves, clustered together in the canopy provide high biomass per bite and reduce foraging time, and are thus preferred (Stobbs, 1973).

Tannins, which deter herbivores (Cooper & Owen-Smith, 1985), also slow decomposition rates (Kraus *et al.*, 2003), so will decrease palatability and increase flammability by making more dead fuel available for longer (Grootemaat *et al.*, 2015). Sodium attracts grazers (McNaughton *et al.*, 1997), and silica is thought to deter grazers (Massey *et al.*, 2009) but these elements have no known impact on fire spread.

Therefore, due to the differences between fire, a physical process, and herbivores, which are biologically metabolising their food, the traits associated with flammability are exactly opposite to those associated with palatability: plants that are very flammable are likely to be largely unpalatable and vice versa (Figure 2, Table 2).

Contrasting resistance and tolerance traits for fire and herbivory in grasses

Key to understanding the response functional traits for resisting and tolerating disturbances is assessment of what plant parts are being protected. Pausas and Lavorel (2003) suggest that a species can persist in an environment exposed to disturbance at an individual, a population, a community, or a landscape level, and propose that the expected traits for persisting at these levels would be very different. An example in fire-prone environments is the distinction between reseeders which die in a fire and reproduce again from seed (population level persistence) and resprouters which persist at an individual level by resprouting from the base or stem after a fire (individual level persistence) (Bond & Midgley, 2001; Pausas *et al.*, 2004).

We suggest that this distinction can be taken further to assess what part of an individual is being protected. This can be leaf material, plant structure, aerial buds, flowering culms, basal buds or root stocks. Resistance strategies thus range from preventing loss of photosynthesis to preventing death (Figure 1), and traits associated with protecting leaf material and aerial meristems are likely to be different from those that protect roots or basal meristems.

For grasses, resistance to fire requires protecting basal buds from heat, and this requires that they are well hidden in dense layers of leaf material (Daubenmire, 1968). This is achieved through intravaginal branching and retained leaf sheaths. Alternatively, erect culms and distal branching result in a flammable aerial leaf material that carries flames away from the base of the plant, achieving high fire resistance for basal buds (Gagnon *et al.*, 2010). (Figure 2 Table 2). In contrast, although resisting heavy grazing also requires protecting basal buds the main risk is uprooting. We propose that a strong root

system (root crown below the soil surface), combined with leaves and culms that break easily (low leaf tensile strength and weak nodes) can protect basal buds from grazing (Table 2).

All traits that allow plants to retain leaf material close to the soil surface (lateral (extravaginal) branching, prostrate culms, rooting at the nodes, basal leaf material) could be considered leaf-level resistance traits against grazing (Figure 2, Box 2). The lack of leaf abscission allows plants to retain dead leaf material, and has been demonstrated to protect new leaves from grazing (Mingo & Oesterheld, 2009), and some grasses (e.g. *Pennisetum mezianum*, *Triodia basedowii*) retain hard spikey culms above-ground as a defensive structure to prevent loss of aerial leaf material (O'Reagain & Mentis, 1989; Drescher *et al.*, 2006). This physical defence would also be termed "resistance" in our framework as it protects palatable leaf material from being eaten.

Large bud banks and high photosynthetic rates enable rapid recovery post-fire and promote fire-tolerance. These would also promote grazing tolerance, but to prevent death under a patchy, chronic disturbance like grazing, having large stored reserves is another key individual-level tolerance trait (Table 2).

Population-level persistence in fire-prone environments requires preventing seeds from being burned, and rapid germination and recruitment after fire. This is promoted by early seed-set and seed release, smoke-stimulated germination, and seed dormancy (Pausas 2018). Tall culms with wind dispersed seeds promote long-distance dispersal that would enable landscape-level persistence (Boucher 2017). In grazed environments rapid clonal growth (through lateral spread and rooting at the nodes) promotes population-level persistence. Ectozoochory, or edible inflorescences and endozoochory (Janzen, 1984) would be strategies for persisting at a landscape level in a grazed environment.

Clearly resprouting and rapid growth after defoliation are shared individual-level tolerance traits for fire and grazing, but the resistance traits are often incompatible (Table 2, Figure 2) – with lateral growth being a good way to hide from grazer mouthparts, and vertical growth being a good way to reduce heat at the soil surface.

Appendix 1 summarises available evidence linking each trait to the functions proposed here, and how to measure it.

Life history strategies in consumer-controlled environments

239 The information presented above supports the idea that avoidance and tolerance should be alternative
240 life-history strategies (van der Meijden *et al.*, 1988; Schwilk & Ackerly, 2001). It also aligns with recent
241 evolutionary theory showing that 'mixed strategies' – involving particular combinations of traits
242 associated with attraction vs resistance vs tolerance – could also be evolutionarily stable (Núñez-Farfán
243 *et al.*, 2007; Carmona & Fornoni, 2013). However, considering fire and herbivory together adds a layer of
244 complexity, as plants with traits that enable avoidance of grazing automatically become more
245 flammable, and vice versa.

246 When one considers fire and herbivory traits together in the context of the three axes: attraction-
247 avoidance, resistance, and tolerance (Figure 3) we expect that that:

248 • Traits that confer flammability and those that confer palatability are very different from each
249 other. Therefore, a life history strategy that avoids defoliation by animals will make a plant more
250 likely to be burned in fire.
251 • Protection from fire (aerial leaf material, keeping buds tightly inside culms) is not the same as
252 protection from grazing (maintaining leaf material below graze height, using extravaginal
253 branching to spread laterally). Therefore extremely fire-resistant grasses are likely to be less
254 grazing-resistant, and vice-versa.
255 • Maintaining fitness after a defoliation event (tolerance) is most important for plants with
256 intermediate levels of attraction and resistance, because these plants are likely to be exposed to
257 highest levels of defoliation.

258 From this four grass life-history strategies emerge (Figure 3):

259 1: Fire resistor, grazer avoider – these plants are likely to be flammable both because avoiding grazing
260 results in more flammable canopies, and because fire resistance traits can increase flammability
261 (Gagnon *et al.*, 2010).

262 2: Grazer resistor, fire avoider – these plants are likely to be palatable both because avoiding fire results
263 in more palatable canopies (Figure 2), and possibly because palatability itself can be advantageous as a
264 mechanism to prevent over-shading by competitors (Belsky *et al.*, 1993), or to increase nutrient
265 availability (de Mazancourt *et al.*, 2001).

266 3: Generalist tolerators – that are unlikely to withstand high levels of grazing or fire, but can tolerate
267 both consumers to some degree. This is strategy is possible because the ability to resprout (stored

reserves and a substantial bud bank of basal meristems at ground level) is effective for both fire and herbivory.

4: Generalist avoiders – these plants do not need to be fire or grazing tolerant as they are unlikely to be exposed to these consumers. However, they are also unlikely to be competitive because avoiding both fire and grazing requires extreme leaf traits and architectures that do not favour carbon gain.

Assessing the range of growth forms that exist in tropical grasslands indicates that examples of these four life history strategies can be found, but that there are often multiple ways to achieve the same functional outcome (Table 3). For example, there are at least three different growth forms of grazing resistant grasses (Hempson *et al.*, 2015): mat-forming stoloniferous/rhizomatous grasses, cushion forming grasses that have their culm bases below ground and are impossible to uproot, and cage-like, stemmy architectures that protect leaf material in the same way spiny trees do. Moreover, grasses can achieve fire resistance through spreading fire up and away from basal meristems (Gagnon *et al.*, 2010), or by protecting meristems in dense basal tussocks (Trollope *et al.*, 2002). The generalist tolerance strategy can be achieved through stored reserves and a physiology that enables continued regrowth despite substantial loss of photosynthetic tissue (McNaughton, 1983; Tiffin, 2000). However, there are many plants that tolerate both fire and herbivory through having flexible growth forms – growing laterally when exposed to herbivory, and growing vertically when ungrazed and burned (Hempson *et al.*, 2015). This phenotypic plasticity represents a second generalist tolerator life history.

We have identified ~8 growth forms (Table 3) which could be effective in consumer controlled ecosystems) which are by no means a complete set: the universality of these growth forms needs to be tested with data from a wide range of grassy ecosystems. The growth form that dominates in a particular environment will depend on the degree of grazing or fire, as well as other environmental constraints plants are placed under (Coley *et al.*, 1985). For example, in very mesic environments carbon is less limiting than nitrogen or phosphorus, so there could be selection for tall, stemmy, carbon-rich, architectures that promote height gain. These growth forms are also more flammable, so the fire resistor/grazer avoider strategy would be common. In arid environments light competition is less severe, so the generalist avoider strategy might be able to persist, despite the reduced growth rates associated with small, sparse canopies. Very cold environments might not be conducive to extravaginal branching or distal tillering which exposes buds, but a dense tussock growth form could confer both fire and cold-tolerance. The flexible growth-form switcher strategy is likely to be most effective in places where the consumer shifts from fire to herbivory over time, whereas the generalist tolerator (compensator)

strategy is predicted to be effective when exposed to persistent but intermediate levels of either consumer. Nutrient rich environments also probably enable the compensator strategy that requires high rates of regrowth and productivity. Moreover, seasonal aridity determines how effective fire-avoidance can be. Only in places without seasonal aridity can plants maintain a high leaf moisture content all year– consequently in temperate places, we expect fire avoidance and grazing tolerance is the most common strategy.

Many of these predictions fit with what has been observed by existing global analyses of grazing traits (McIntyre *et al.*, 1999; Diaz *et al.*, 2007), however, here fire is explicitly integrated into the same predictive framework.

Contrasting the strategies identified here with the classic "Increaser/Decreaser" strategy framework (Foran *et al.*, 1978) often used in southern African grasslands demonstrates the value of our conceptual model. "Increaser 2" species are defined by Foran *et al* (1978) as those that increase when landscapes are heavily grazed. Ecologically this could occur because they are unpalatable and avoided by grazers (*Aristida congesta*), or because they are palatable and resistant to grazing (*Pennesitum clandestinum)*. From a land management point of view it is essential to distinguish these two functional groups because one is desirable to a cattle farmer, and the other not.

Ecological and evolutionary implications

When ordering grass communities across a 'consumer' gradient from frequent fire to intense grazing one expects turnover in the functional types that persist and dominate (Figure 4). As the generalist strategies are only effective at intermediate levels of fire and herbivory, the prediction would be that there is higher functional diversity in these environments, and that fewer strategies should exist in extreme fire and extreme grazing situations. For the same reason we would also expect generalist species to have larger range sizes. Figure 4 predicts that high grazing can potentially result in two distinct ecosystem states: grazing lawns (McNaughton, 1984) or systems where only generalist avoiders can persist. There is ample field evidence for these two different grazing end-points (Mack & Thompson, 1982; Milchunas *et al.*, 1988), and understanding the conditions that result in each state is an important management issue.

The axis from fire to grazing (Figure 4) can occur across regional gradients, where fire-prone mesic ecosystems transition into to grazer-dominated ecosystems at lower rainfalls (Bond, 2005; Archibald & Hempson, 2016). However, it is also possible for feedbacks between grass communities and their consumers to maintain either fire-adapted or grazer-adapted grasslands within a single landscape (Hempson et al. TREE in press). Here the genetic pool of grasses is similar, and differentiation occurs through filtering of grass functional types, and through feedbacks to consumer regimes. Because grazing promotes low-statured grasses with leaf traits that deter fire, and fire promotes tall-statured grasses with leaf traits that deter herbivores (Figure 2, Table 2), these habitat types should be quite distinct in terms of species composition. If the grasses in grazing lawns are also phylogenetically distinct from those in surrounding tall grass landscapes, this would be strong evidence for different evolutionary origins of fire vs herbivore-adapted ecological strategies. Alternatively, grasses from all lineages have the capacity to evolve fire and herbivore-tolerance, in which case these communities would not show strong phylogenetic patterns.

Field data indicate that geographically distant grasslands show similar functional and phylogenetic responses to changes in fire regime, but divergent responses to changes in grazer regime (Forrestel *et al.*, 2014, 2015). This implies that grazer adaptations vary more between regions than fire adaptations, and are dispersed more widely in the phylogeny, a hypothesis that can now be tested using the traits and life-history strategies identified here. Different suites of grazers, with different feeding ecologies, evolved independently across the globe (Owen-Smith, 2013), whereas fire regimes are an outcome of climate and fuel properties and will converge in conditions where these are similar (Archibald, 2013). Demonstrated links between fire and grasses of just one lineage – the Andropogoneae - support this (Ripley *et al.*, 2015; Simpson *et al.*, 2016).

Moreover, plant height is a key plant functional trait (Westoby, 1998; Díaz *et al.*, 2016) and selection for a vertical (fire resistor) vs lateral (grazer resistor) growth, will have consequences for light competition as well as other aspects of plant life history. For wind-pollinated plants like grasses height affects gene flow and dispersal distance (Rodger *et al.*, 2018), with consequences for plant range size, and rates of speciation (Boucher *et al.*, 2017). We would therefore expect that grazer adapted grasses should have smaller ranges overall, although this would depend on dispersal mode.

It is important to recognise that fire is not actually a very strong filter for grasses: the absence of wood, and concentration of meristems at/below the soil surface mean that most fires burn material that is already dead and ready to be discarded (slow creeping back-fires (Trollope *et al.*, 2002) are the

exception here and might be the selective force behind leaf-sheath retention and dense basal tussocks). Individual-level resistance to fire therefore becomes less important than community-level processes after the fire (Pausas & Lavorel, 2003). Grass species with high growth rates and rapid height gain are effective competitors for space and light in the high-resource environment after a fire, and these tall grasses are more flammable (high rates of biomass accumulation and connected fuels). Thus, tall grasses competing for light reinforce a fire feedback to increase flammability (D'Antonio & Vitousek, 1992; Rossiter *et al.*, 2003). High-fire environments therefore exclude other herbaceous growth forms more through competition and shading than through the frequency of fire, whereas it is the fire itself that excludes many woody growth forms from these ecosystems.

We therefore expect:

1. Lower functional diversity in extreme fire/grazing situations, with highest functional diversity in systems with both consumers. This does not necessarily translate into higher species richness, as that will depend on evolutionary processes related to diversification rates and dispersal.
2. Turnover in life-forms and species across regional-scale gradients will be reflected at a landscape-scale between heavily grazed and frequently burned patches. These will emerge due to reinforcing feedbacks: palatable grasses are not flammable, and fire-resistant grasses are not necessarily grazing-resistant.
3. Grazer-adapted grasses are phylogenetically distinct from fire-adapted grasses, and likely more widely dispersed across the phylogeny. This is because of the wider diversity of grazers globally.
4. Laterally-spreading, grazer-adapted life histories will impose constraints on gene-flow and dispersal that will increase speciation rates and reduce species range sizes.
5. The annual "generalist avoider" life-history strategy is one outcome of intense heavy grazing, but not the only one. There is a wide range of grazer-adapted life histories within perennial grasses that has so far not been elaborated.

Discussion

We have demonstrated here that making sense of the ecological strategies found in consumer-controlled environments requires integrating understanding across disciplines. In particular, in grasslands it is only possible to develop clear predictions around community assembly and evolution when the drivers of fire and large mammalian herbivory are considered together, because adaptations

for one type of consumer can affect how susceptible plants are to other consumers. We therefore advocate that datasets on fire and grazing traits be collated and the expected relationships tested.

Key to integrating fire ecology and trophic ecology was developing a theoretical framework related to attraction/avoidance, resistance, and tolerance of consumption (Figure 1). This framework blends aspects of previous conceptual models, but makes a strong distinction between resistance traits (that act while a plant is being consumed), and attraction/avoidance traits (that determine whether plants are likely to be consumed in the first place). Moreover, it also forces trophic ecologists to raise questions about the degree to which palatability can be selected for – something fire ecologists have been grappling with for years.

Once fire and herbivore adaptations can be placed on common axes (Figure 3), it is possible to assess the degree to which they are correlated or antagonistic. In this example we show clearly that fire and herbivore adaptations in grasses are often contradictory: that flammable grasses are not palatable, and that grazing-resistant grasses are not necessarily fire-resistant (Figure 2, Table 2). This then results in expectations about the dominance of different grass life history strategies across environmental gradients, and also the degree to which fire and herbivory can shape ecosystems and act to re-inforce particular consumer regimes through altering species composition.

It would be good to ask similar questions regarding fire and herbivory adaptations in trees and non-grass herbaceous species, and to expand this thinking to other consumers such as insect herbivores. Testing this framework in these different contexts will demonstrate its universality.

The tolerance strategies associated with different positions on the avoidance-attraction continuum have already been identified for trees (Figure 3). For example in pines there is correlated evolution in traits associated with attracting and tolerating vs avoiding and resisting fire (Schwilk & Ackerly, 2001; He *et al.*, 2012). Moreover, within savanna trees it has been shown that growth forms associated with resisting herbivory can make trees less resistant to fire (Archibald & Bond, 2003), and that this can result in sorting of savanna tree communities in space (Charles-Dominique *et al.*, 2015; Osborne *et al.*, 2018), and over time (Staver *et al.*, 2007) as the consumer changes. Thus one of the major predictions of this framework appears to hold true for woody species.

It has always been difficult to fit life history strategies associated with herbivory and fire into classic ecological theory (Bond & Midgley, 2001; Pausas & Keeley, 2014). The ruderals in Grime's (1977) CSR scheme are predicted to occur in highly disturbed environments, but this strategy represents only

418 population-level persistence and cannot encompass the full spectrum of strategies described here
419 (Figures 1,3). However, as discussed above, it should be possible to make predictions about what
420 combination of avoidance, resistance and tolerance traits are more likely for plants in different
421 environments, and these need to be reconciled with the strategies identified for carbon capture, water
422 and nutrient use efficiency, and reproduction in the same environments. For example, avoiders, which
423 have defensive chemicals in their leaves, have been shown to characterise Grimes's 'stress-tolerator'
424 strategy because protecting leaf and above-ground biomass is important when this biomass is hard-won
425 (Coley *et al.*, 1985).

426 Many of the traits we discuss here in the context of fire and herbivory are also considered important in
427 the broader trait and plant economics literature, such as C:N ratio and plant height (Westoby, 1998;
428 Wright *et al.*, 2004; Díaz *et al.*, 2016). However, classic leaf trait data are not sufficient to fully quantify
429 consumer-driven life histories, and there is a need for further quantification and empirical testing of
430 these consumer-related traits. To enable this in the supplementary material (SM) we describe sampling
431 protocols for the fire and grazer traits mentioned in Table 2, and contrast them with similar traits in
432 woody plants. We include traits associated with population and landscape-level persistence although we
433 were not able to elaborate on these here.

434

435 **Conclusions:**

436 We have developed a framework for thinking about consumer-driven ecological strategies in terms of
437 three components - avoidance/attraction, resistance, and tolerance. We predicted that successful
438 ecological strategies in consumer-driven environments require unique combinations of traits, i.e. not all
439 parts of this strategy space are occupied, but there are combinations of avoidance, resistance and
440 tolerance traits that will be successful for a particular consumer.

441 We then described grass traits associated with avoidance/attraction, resistance and tolerance of fire and
442 mammalian herbivory, and demonstrated that these are not aligned: i.e. fire-adaptations affect a plant's
443 avoidance, resistance, and tolerance of herbivory and vice versa. We used this information to develop
444 expectations on what types of grass ecological strategies will be successful in environments exposed to
445 both fire and herbivory, and discuss the environmental conditions that are most likely to favour
446 particular strategies; i.e. we expand on Coley's (1985) Resource Availability Hypothesis.

447 This represents a first step towards reconciling two disparate fields of ecology (fire and trophic ecology)
448 that have a lot to offer each other. It provides tools for predicting both the diversity of life history
449 strategies and the plant species diversity under different consumer regimes.

450

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460 wrote the manuscript with contributions from GPH and CL. GPH perfected the figures.

461

462 Table 1: Summarising the different ways that terms associated with fire and herbivore adaptations have
463 been used in key texts and how we define them here.

464

	Crawley 1983 and Belsky *et al.* 1993	**Rosenthal & Kotanen 1994**	**Stowe *et al.*, 2000**	**Briske 1996**	**Strauss & Agrawal 1999**	**Pausas & Lavorel 2003**	**In this manuscript**
Degree to which a plant is palatable or flammable	Resistance (Avoidance)	Avoidance	Resistance	Avoidance (biochemical)	Resistance	Resistance	Avoidance
Protecting plant parts during a defoliation event	Resistance (Avoidance)	Avoidance/ Tolerance	Resistance	Avoidance (morphological)	N/A	Avoidance/ tolerance	Resistance
Ability to regrow lost biomass/recover fitness following a consumption event	Resistance (Tolerance)	Tolerance	Tolerance	Tolerance	Compensation/ Tolerance	Resprouting capacity	Tolerance (individual-level persistence)
Ability to recover from seed following a consumption event	N/A	N/A	N/A	N/A	N/A	Population level persistence	Population level persistence
Ability to take advantage of space/resources following a consumption event)	N/A	N/A	N/A	N/A	N/A	Community level persistence	Tolerance
Ability to recolonize via dispersal following a defoliation event.	N/A	N/A	N/A	N/A	N/A	Landscape level persistence	Landscape level persistence

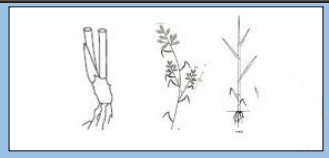
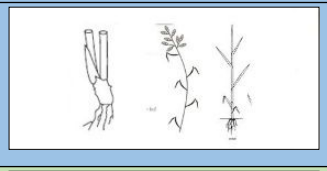
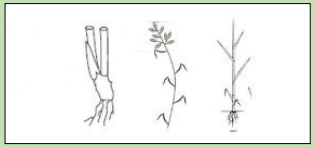
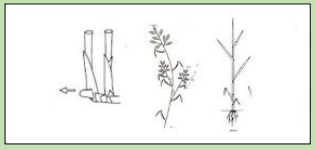
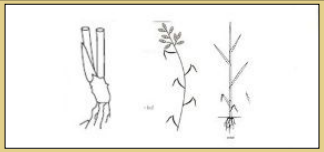
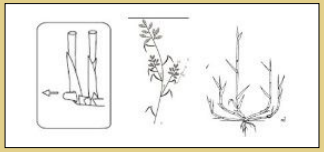
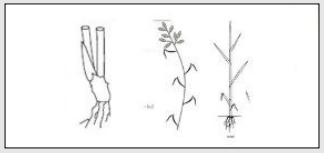
465

466

Table 2: Key grass traits associated with attraction/avoidance, resistance, and tolerance of grazing vs fire. Items coloured blue represent traits that are compatible (i.e. are shared for grazing and fire), and red traits that are antagonistic (i.e. are opposed for grazing and fire). Traits listed in the attraction/avoidance section are those that maximise the attractiveness of grasses to either grazers or fire. Generalist strategies that work for both consumers are possible in terms of tolerance, but less so for resistance and avoidance.

	Grazing	Fire
Attraction/avoidance traits (palatability/flammability)	Low C:N ratio High bulk density High leaf moisture content Low tannin content High phosphorus content Large leaves High salt content Low silica content	High C:N ratio Low bulk density Low leaf moisture content High tannin content Low phosphorus content Thin leaves High biomass
Resistance traits	Meristems at/below the soil surface Lateral growth (extravaginal branching, prostrate culms, stoloniferous/rhizomatous) Strong root system which prevents uprooting Leaves and culms with low tensile strength (alternatively) Spikey hard culms/spines that protect aerial leaf material.	Meristems at/below the soil surface Vertical growth (intravaginal branching, erect culms, short rhizomes) Distal tillering to move flames away from the basal meristems Retain leaf sheaths to protect buds
Tolerance traits (individual level persistence)	Rapid resprouting/large bud bank Substantial stored reserves	Rapid resprouting/large bud bank
Population-level persistence traits	Geniculate growth form (flowers not eaten) Clonal growth (rooting at nodes)	Early seed set and release (before fire season) Smoke stimulated germination Seed dormancy
Landscape-level persistence traits	Good dispersal ability (especially ecto- and endozoochory) Rapid germination and establishment Short generation times	Good dispersal ability (especially wind dispersal) Rapid germination and establishment Short generation times

475 Table 3: There are theoretically four distinct life-history strategies associated with fire and grazing. These are exemplified in ~8 different growth forms that are
476 common in tropical grassland flora, each associated with particular combinations of plant traits (Box 2) that result in unique architectures.

Life history strategy	Potential growth forms	Examples	Image	Key traits
1: Fire resistor, grazer avoider.	Aerial flammable tussocks - with vertical growth, and distal tillering that maintains flames above the soil surface (fire-resistance largely achieved through being flammable).	*Hyparrhenia filipendula, Schizachyrium sanguineum*		
	Basal resistor tussocks - with vertical growth and dense intravaginally branched culms that protect buds from fire (fire resistance largely achieved through protecting basal meristems).	*Panicum natalense, Alloteropsis semialata, Aristida junciformis*		
2: Grazer resistor, fire avoider	Mat-forming lawn grasses - with extravaginal branching, laterally-growing stems, and palatable high-density leaves (require grazing to avoid self-shading and prevent being out-competed).	*Stenotaphrum secundatum, Cynodon dactylon*		
	Cushion-forming grasses - maintain culms and leaf bases below the soil surface, leaving palatable leaf blades within graze height (require grazing to avoid self-shading and prevent being out-competed).	*Sporobolus nitens, Microchloa kunthii*		
	Stemmy, cage-like architecture that protects green leaves from being eaten.	*Pennisetum mezianum, Triodia basedowii*		
3: Generalist tolerators	Compensators: tussock grasses that can resist uprooting and have stored reserves, and thus persist when lightly/briefly defoliated.	*Themeda triandra, Heteropogon contortus, Digitaria eriantha*		
	Growth-form switchers - that can grow laterally with stolons when grazed, but grow vertically in tall, fire-prone communities.	*Urochloa mosambicensis, Panicum coloratum*		
4: Generalist avoiders	Sparsely branched tussocks with thin leaves, low productivity, and low bulk density.	*Aristida congesta, Eragrostis rigidior*		

Box 1: Resolving terminology

There is no consistent terminology for discussing fire and herbivory functional traits. Here we set up the definitions we will use for this paper and discuss how these contrast with those used by other researchers.

BEFORE DEFOLIATION OCCURS:

Palatability: Having leaf material that is preferred by grazers

Flammability: Having leaf material that is easily ignited and carries a fire

Avoidance: Having leaf material that is not preferred or easily ignited. We take a constrained definition here where avoidance refers to a mechanism for avoiding the probability of being exposed to a stress via low palatability or low flammability. Traits that reduce the impact of a stress when it occurs (e.g. mechanical plant defence strategies such as spines or thick bark) confer resistance and are considered elsewhere. In this we differ from other key references such as Briske (1996), but the reasons for this break from tradition will become evident.

Plants therefore exist on a continuum of **avoidance vs attraction** of defoliation. Plants that are "attractive" to grazers are termed palatable, and plants that are "attractive" to fire are termed flammable. The traits associated with this continuum could be considered *effect traits* sensu Lavorel and Garnier (2002).

DURING DEFOLIATION:

Resistance: the ability to protect certain plant parts from being lost. Depending on the ecological strategy of the plant this could be leaf material, structural material (stems/branches), or basal buds/roots, and the resistance strategy defines the degree to which the plant will need to recover from/compensate for a defoliation event. In this we diverge from Strauss and Agrawal (1999) who use the term resistance in the same way we use avoidance.

AFTER DEFOLIATION/DURING THE LIFETIME OF THE PLANT:

Tolerance: the ability to survive defoliation and to reproduce/spread while exposed to defoliation. In this we are aligned with Strauss and Agrawal (1999) who define it as "the degree to which plant fitness is affected by herbivore damage relative to fitness in the undamaged state". Highly tolerant plants survive and spread under higher levels of consumption. We also consider competitive ability (i.e. the ability to capture space/resources and benefit from a defoliation event) to be a component of this (Pausas & Lavorel, 2003).

OVER EVOLUTIONARY TIMESCALES:

Persistence: whether or not a species is found in a system exposed to fire/herbivory. This can occur at an individual, population, or landscape (species) level (Pausas and Lavorel 2003). At an individual level it is a synonym for tolerance.

Box 2: Traits associated with fire/grazing adaptations

Bud position: Grasses have a hemicryptophyte life form with perennating organs at or close to the soil surface, but there is variability in where the buds form. When buds are maintained below the soil surface they are more resistant to uprooting by grazers and protected from fire.

Culm orientation: Vertical growth increases height gain and light capture and moves flammable material away from the sensitive buds, horizontal growth enables lateral spread and keeps palatable material out of reach of grazers. This trait is very flexible within species (Kellogg, 2015) and over the lifetime of an individual.

Distal tillering (also called aerial branching): Distal tillering enables space-filling by initiating new shoots from the nodes of existing culms: it increases light capture and aerial biomass for vertically-growing grasses, and is necessary for the branched growth form of mat-forming grasses (Kellogg, 2015).

Stemminess: Thick, woody culms enable height gain, and when associated with distal tillering can create a cage-like architecture. Moreover some grass species also have spines which achieve the same effect (Clayton *et al.*, 2014). Like spines on trees these stems increase resistance of certain grass species to grazing (O'Reagain & Mentis, 1989).

Extra vs intravaginal branching: Tillers produced from intravaginal branching result in a caespitose architecture that enables height gain and protects basal buds within layers of leaf sheaths in a dense basal tussock. Tillers produced through extravaginal branching enable space-filling and lateral growth, but expose buds: the stolons of mat-forming grasses form from extravaginal tillers.

Storage: Some grasses, mostly pooids, have below-ground storage organs of modified leaves or stems (Kellogg, 2015). Rhizomes, stolons, and roots store sufficient reserves for rapid resprouting after once-off defoliation in most species, but a truly tolerant plant that can persist in the face of repeat defoliation would need to maintain a positive carbon balance, and could not depend on stored reserves (Belsky, 1986).

Photosynthetic pathway: The high C:N ratio that strongly correlates with flammability is to some degree a consequence of C4 photosynthesis but this is an over simplification: flammable C3 species with high C:N ratios, and palatable C4 species with low C:N ratios exist.

There is much phylogenetic sorting of the key traits mentioned above: Distal tillering is unknown in all pooideae grasses, but is common in Panicoids and particularly common in Andropogonoids (Kellogg, 2015). Buds below the soil surface and rhizomes are ancestral to Poaceae. Moreover, extravaginal branching is also the ancestral trait (Linder et al. 2017), although the tussock, intravaginally branched growth form is far more common currently across Poaceae (Kellogg, 2015).

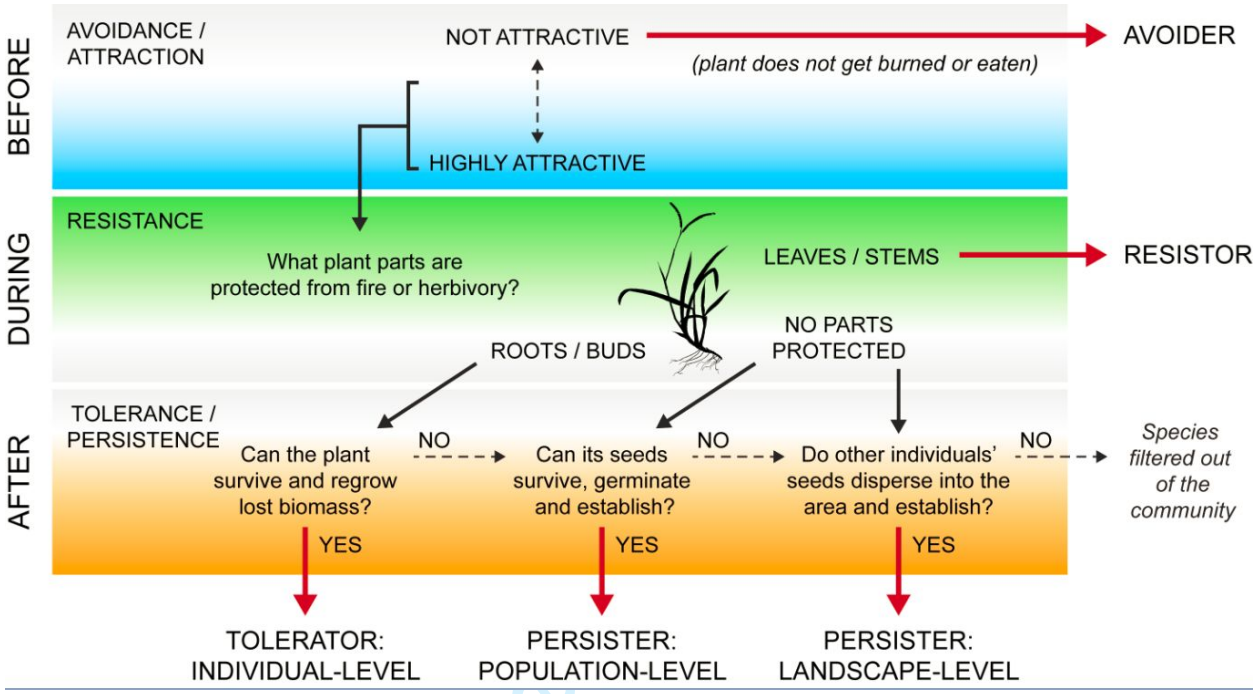


Figure 1: Describing how traits associated with avoidance, resistance, and tolerance act across time periods and scales (plant part, individual, population or landscape) to filter plant communities. Different axes, associated with different plant traits, operate before, during, and after defoliation. If a plant has the right combination of avoidance, resistance, and tolerance traits then it can persist in a community, otherwise it is filtered out. In this formulation resistance is a prerequisite for tolerance but the degree of resistance determines the level of tolerance required (i.e. this doesn't contradict trophic ecology theory). See Figure 3 for an example of how this scheme can be applied to predict grass life history strategies for fire and grazing.

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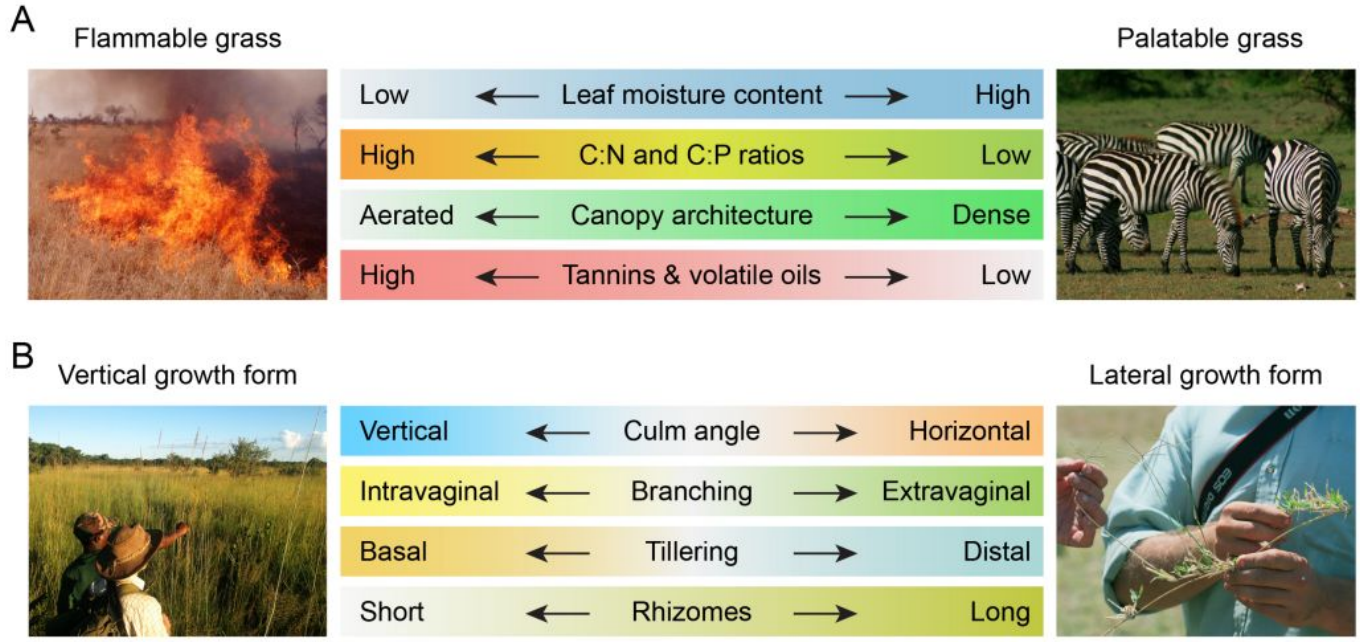

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566 Figure 2. A: Contrasting flammable and palatable grass traits. Due to the differences between fire, a
567 physical process, and mammalian herbivores, that biologically metabolise their food, the traits
568 associated with palatability are opposite to those associated with flammability, and plants that are very
569 flammable are likely to be largely unpalatable. B: Contrasting the traits associated with vertical and
570 lateral growth in grasses: due to differences in the traits required to resist herbivore mouthparts vs hot
571 flames grazer adapted grasses tend to grow laterally whereas fire-adapted grasses tend to grow
572 vertically.

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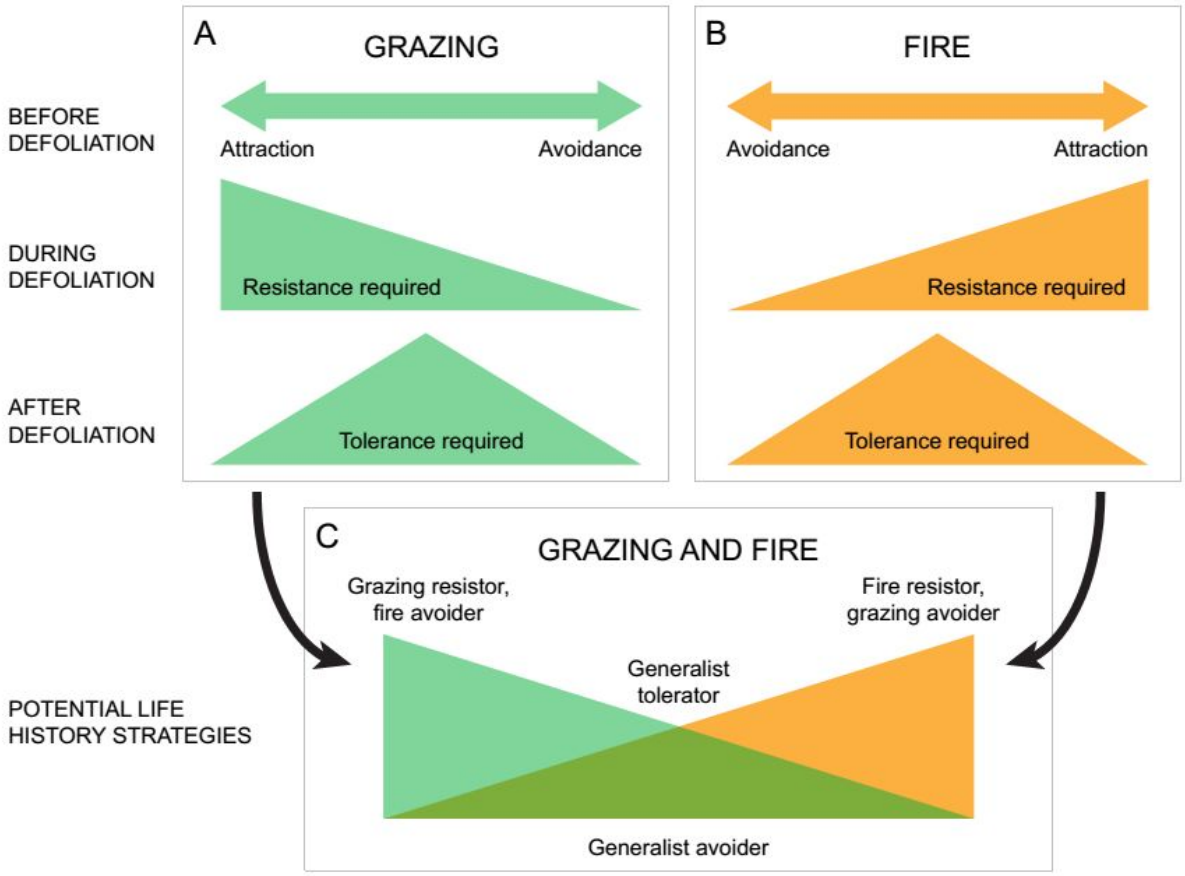

Figure 3: Four potential life history strategies emerge when fire and grazing traits are compared on axes associated with avoiding, resisting, and tolerating fire and herbivory. Key to this model is the fact that traits associated with flammability are different from those associated with palatability. Likewise, because fire resistance traits are different from grazing resistance traits, there is no generalist resistor strategy, but there can be a generalist tolerator strategy.

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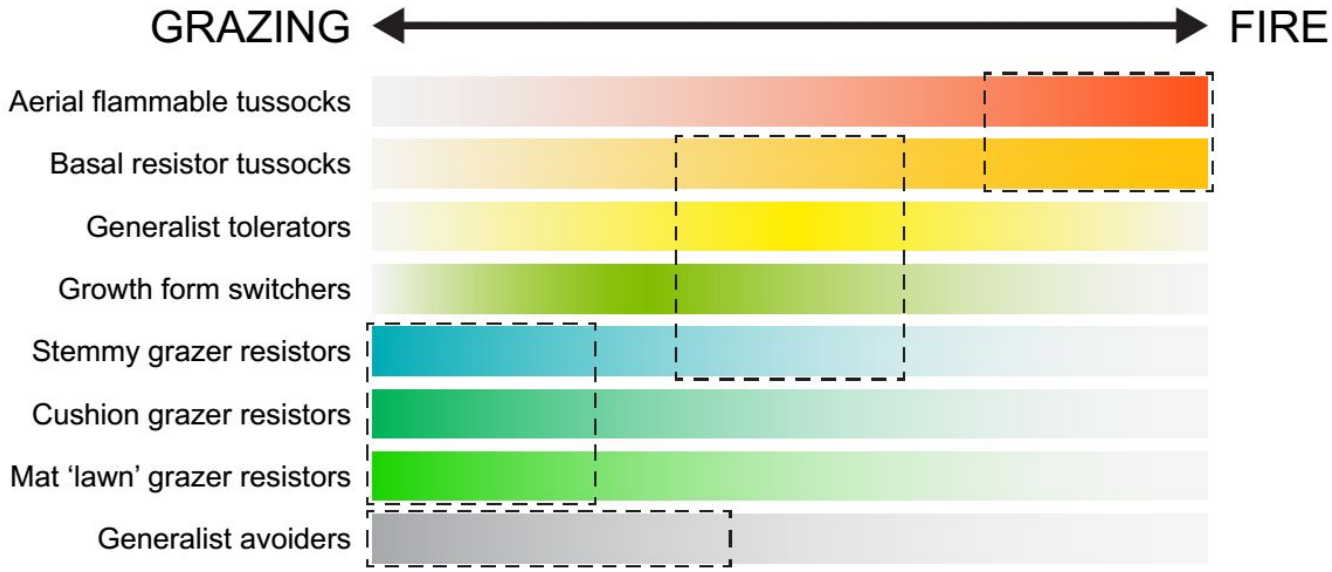

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595 Figure 4: Showing how functional composition is expected to change across a 'consumer' gradient from
596 frequent fire to intense grazing. Higher functional diversity is expected in environments with both
597 consumers present. These different communities could be found within a single landscape (e.g. Arnold
598 *et al.* 2014), or across the regional tropics – where fire-prone mesic ecosystems give way to grazer-
599 dominated ecosystems at lower rainfalls (Archibald & Hempson, 2016). High grazing can potentially
600 result in two ecosystem states: grazing lawns, or systems dominated by generalist avoiders. Generalist
601 avoiders are unlikely to dominate in high fire environments as they are inferior competitors.

602

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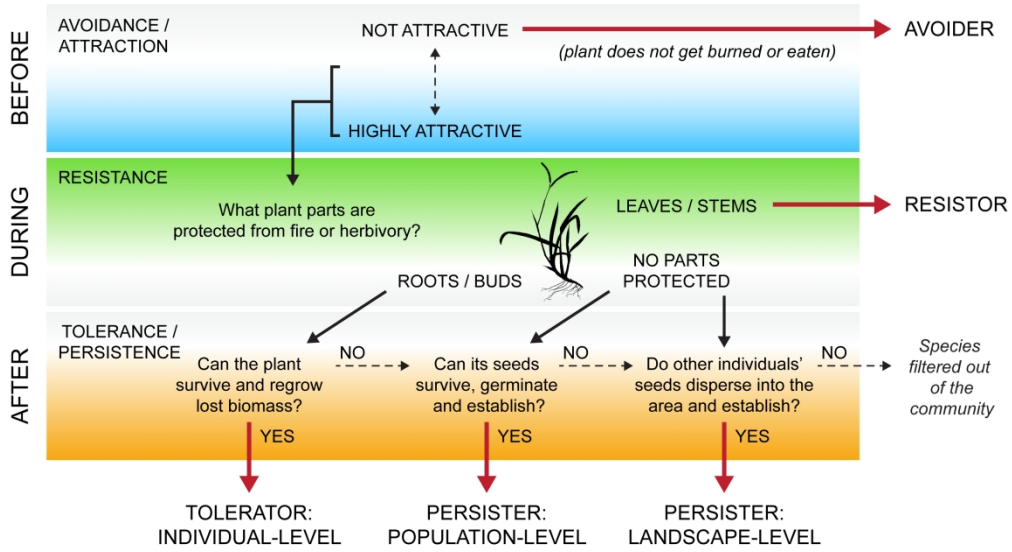

Figure 1: Describing how traits associated with avoidance, resistance, and tolerance act across time periods and scales (plant part, individual, population or landscape) to filter plant communities. Different axes, associated with different plant traits, operate before, during, and after defoliation. If a plant has the right combination of avoidance, resistance, and tolerance traits then it can persist in a community, otherwise it is filtered out. In this formulation resistance is a prerequisite for tolerance but the degree of resistance determines the level of tolerance required (i.e. this doesn't contradict trophic ecology theory). See Figure 3 for an example of how this scheme can be applied to predict grass life history strategies for fire and grazing.

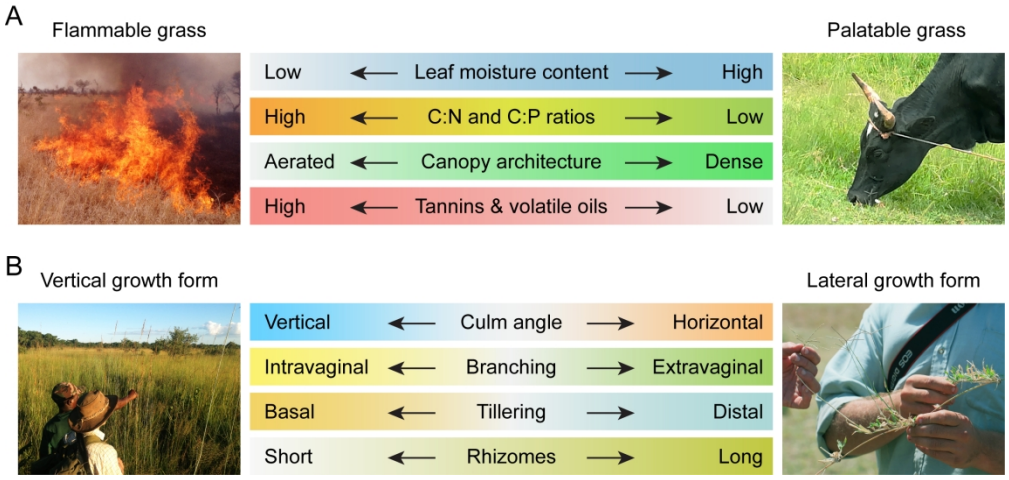

Figure 2. A: Contrasting flammable and palatable grass traits. Due to the differences between fire, a physical process, and mammalian herbivores, that biologically metabolise their food, the traits associated with palatability are opposite to those associated with flammability, and plants that are very flammable are likely to be largely unpalatable. B: Contrasting the traits associated with vertical and lateral growth in grasses: due to differences in the traits required to resist herbivore mouthparts vs hot flames grazer adapted grasses tend to grow laterally whereas fire-adapted grasses tend to grow vertically.

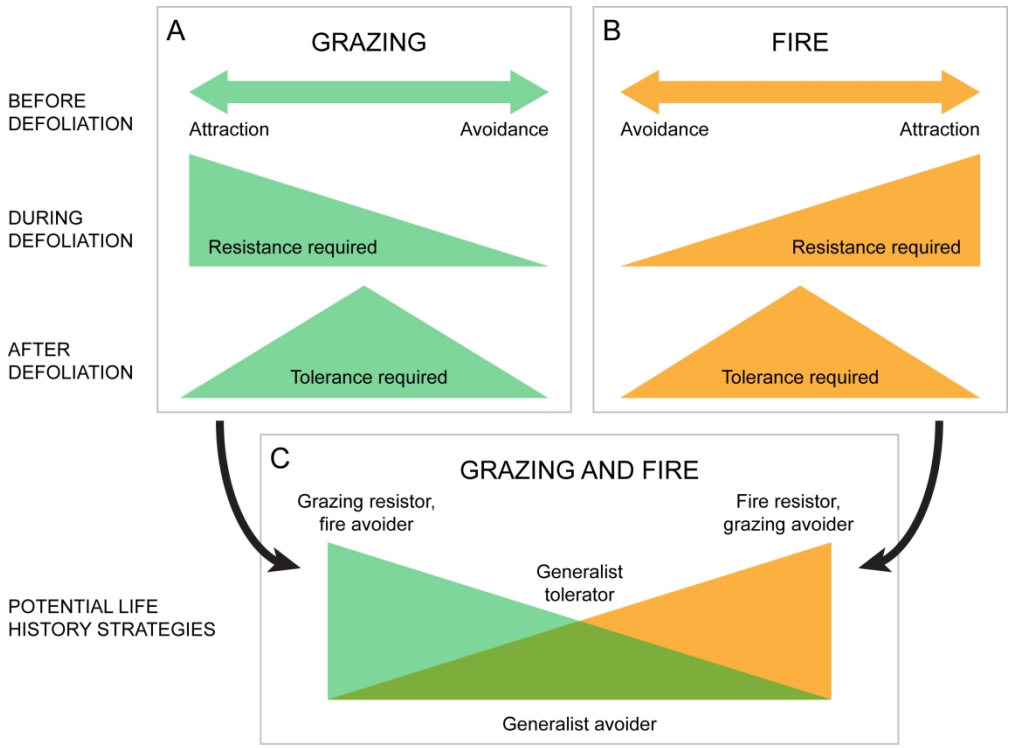

Figure 3: Four potential life history strategies emerge when fire and grazing traits are compared on axes associated with avoiding, resisting, and tolerating fire and herbivory. Key to this model is the fact that traits associated with flammability are different from those associated with palatability. Likewise, because fire resistance traits are different from grazing resistance traits, there is no generalist resistor strategy, but there can be a generalist tolerator strategy.

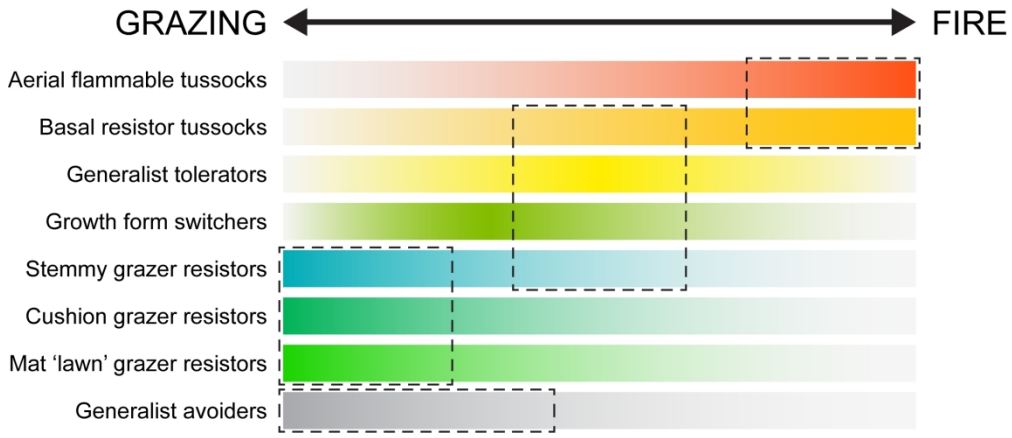

Figure 4: Showing how functional composition is expected to change across a 'consumer' gradient from frequent fire to intense grazing. Higher functional diversity is expected in environments with both consumers present. These different communities could be found within a single landscape (e.g. Arnold et al. 2014), or across the regional tropics – where fire-prone mesic ecosystems give way to grazer-dominated ecosystems at lower rainfalls (Archibald & Hempson, 2016). High grazing can potentially result in two ecosystem states: grazing lawns, or systems dominated by generalist avoiders. Generalist avoiders are unlikely to dominate in high fire environments as they are inferior competitors.